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A FOSSIL SEQUOIA FROM THE SIERRA NEVADA.[1]

EDWARD C. JEFFREY.

(WITH PLATES XVIII AND XIX)

AMONG the material of fossil woods stored in the basement of the Botanical Museum of Harvard University is a large piece from the line of the Central Pacific Railway. It is catalogued as no. 7354 and is described on the label as "From tunnel no. 1, Central Pacific R. R., Blue Gap, Sierra Nevada Mountains. Elevation above the sea 4520 ft. Found under 60 ft of conglomerate." There is no further information as to the time of its collection or the formation from which it was derived. As the piece of wood in question had the color and general texture of a Sequoia, I was led to investigate its microscopic structure, with the result that it turned out to be a new species of the genus, presenting a number of interesting and novel features.

Dr. F. H. KNOWLTON, of the United States Geological Survey, has expressed the opinion that the wood which forms the subject of the present article is of the age of the auriferous gravels, *i. e.*, Miocene; but is unable to state positively that this is the case, on account of the absence of definite evidence. As the location of the specimen is clearly indicated, it will probably be an easy matter to determine subsequently its exact geological horizon. In any case the morphological features which it presents are of sufficient interest to justify a description at the present time.

The fragment of wood in its original condition as taken from the collection was about 1.5 m long. One end was much frayed and

[1] *Contributions from the Phanerogamic Laboratories of Harvard University.* No. 1.

water-worn; the other showed a fractured surface as if it had been broken away from a longer piece. This supposition is strengthened by the fact that there are a few ax marks on the broken end of the specimen. The piece measured about 15^{cm} in the radial direction and about 18^{cm} tangentially, and is rounded in these directions apparently by water carriage. There are about three hundred rings of growth, and perpendiculars drawn from these show that the original trunk of which the specimen under discussion is a fragment must have been at least six feet in diameter. It was possibly much larger, since in all probability a good deal of ligneous tissue has disappeared from the outer surface of the specimen. The wood had undergone comparatively little alteration from decay, and the fact that it is only very slightly impregnated with silica, easily removed with hydrofluoric acid, makes it very favorable for investigation. The preservation even of minute details of structure is far beyond that of any other fossil Sequoia with which I am familiar.

Fig. 1 shows some of the characteristic features of a transverse section of the fossil wood under discussion. The annual rings are well marked and very regular even in sections of greater area than that shown in the figure. Two peculiarities stand out above all others in *fig. 1*, viz., the apparent absence of resin cells, such as ordinarily occur in cupressineous woods, and the presence of resin canals in both horizontal and vertical planes, a feature characteristic of the Abietineae and hitherto unknown in the cupressineous series. The rings of growth are mostly composed of thin-walled tracheids, but suddenly toward the outer border of the annual zone appear a few thick-walled tangentially flattened elements. In one of the annual rings may be seen a number of open spaces rounded in outline. These are vertical resin canals in transverse section, and are confined to the spring wood. A very broad horizontal duct originates outwardly from the vertical series of resin canals just described and passes beyond the boundary of the figure. *Fig. 2* shows some thin annual rings highly magnified. The tracheids are more often square than pentagonal or hexagonal in outline. The pits are confined to their radial walls, except in the case of the thick-walled autumnal tracheids, and are obviously in two rows as seen in transverse section. The tangential pits which are sometimes found in the spring wood of the

living Sequoias are not found in the present species.[2] On the left of the figure may be seen a medullary ray. The cells are obviously very long, and in the present instance extend across a complete annual ring. The elements still retain their dark granular contents, the so-called resin globules. In the present species of Sequoia the resinous material is mainly found in the medullary rays and scarcely at all in the wood, in this respect presenting a marked resemblance to Tsuga and Abies among the Abietineae. There is, however, a certain number of resin cells on the outer face of the summer wood. One of these elements is shown in the second annual ring and on the right of the figure. This feature, too, finds a parallel in Tsuga among the Abietineae.

Fig. 3 shows part of a tangential section of the wood of our species, under low magnification. The irregular dark striping of the center of the figure represents the summer wood, while the light-colored lateral portions correspond to the spring wood. Most of the medullary rays appearing in the figure are so small as to be scarcely discernible, but some of them are enormously enlarged to constitute fusiform rays, which contain horizontal resin canals. Most of these canals appear to be empty, but some are obviously filled with coarsely granular contents. The appearance presented in the section shown in our *fig. 3* is somewhat exceptional for the species under discussion. In most cases a tangential section of the wood reveals no fusiform rays and no horizontal resin canals.

Fig. 4 appears to afford an explanation of the peculiarities seen in *fig. 3*. The magnification in this instance is not great, and as a consequence a large number of annual rings are present. These become arched and suffer interruption toward the lower part of the figure. In this case we have obviously to do with a healing wound. The interruption in the continuity of the annual rings indicates the time at which the injury took place, and outside this gap the rings of growth are unusually thick, as is ordinarily the case in traumatic wood. There is a reaction farther out and the rings become much thinner, again to increase their thickness once more still farther out. From the right border of the wound a horizontal

[2] PENHALLOW, D. P., Generic characters of North American Taxaceae and Coniferae. Trans. Roy. Soc. Canada 2:1896.

resin canal can be seen making its way outward through all the annual rings seen in the plane of the figure. By careful inspection it is also possible to make out that there are vertical canals in series in the spring wood of the first ring of ligneous growth subsequent to injury. *Fig. 5* shows part of another section through the same wound more highly magnified. The tangential series of resin canals in the spring growth of the first traumatic ring can now be clearly seen. Passing off from these can be made out three horizontal ducts, the most median of which does not actually communicate with the vertical canals in the plane of the present section. To the right of the figure a short tangential series of ducts can be seen in the second ring of growth formed after the wound. No horizontal canals originate from this weaker series of vertical canals. *Fig. 6* is taken from the center of the wounded region, and the annual rings immediately abutting on the wound are the second and third formed subsequent to the injury. Each of them contains a weak series of vertical canals in the vernal wood, but these do not give rise to any horizontal ducts. *Fig. 7* shows a part of another section through the same wound, somewhat more highly magnified. The vertical canals of the spring wood are now clearly discernible, and from these are passing off in the horizontal direction three huge resin canals. Two of these are more or less completely filled by parenchymatous tyloses.

We are now in the position to discuss the resin canals vertical and horizontal appearing in *figs. 1* and *3*. It is a well-known fact that in the Abietineae the formation of resin canals may be brought about as the result of wounds. The present writer has shown that the same feature is found in the living species of Sequoia.[3] In the existing species of Sequoia the formation of traumatic resin canals is entirely confined to the vertical plane, so far as our present knowledge goes. In those Abietineae which give rise to ligneous resin canals only as a result of injury they are also confined to the vertical plane, except in the genus Cedrus, where, as the present author shows in an article about to be published, they are formed horizontally as well. Three cases of injury have been found in the fossil Sequoia at present under consideration, and in each of the three cases the injuries led to the

[3] JEFFREY, E. C., Memoirs of the Boston Society of Natural History **5**: no. 10.

formation of traumatic resin canals. Where the irritation is most severe, *i. e.*, in the first annual ring formed after injury, there are apt to be both horizontal and vertical canals; while in the later formed rings the impulse gradually dies out and only vertical canals originate. The horizontal canals run in considerable numbers from the margins of healing wounds. *Fig. 3* represents a section through such a patch of traumatic horizontal canals. *Fig. 8* shows the appearance of the large horizontal canal to be seen on the left of *fig. 3* when somewhat more highly magnified. The enormously enlarged medullary ray is almost entirely taken up by the huge resin canal, which in turn is occluded by a mass of cells constituting a tylosis. *Fig. 9* shows a smaller duct from the right of *fig. 3* somewhat more highly magnified than the foregoing. The continuity between the tylosis and the wall of the duct can clearly be made out in this figure. The cells constituting the walls of the traumatic resin canals in the Sequoias are thick-walled and much pitted, and generally contain in greater or less abundance the dark brown masses which occur in the resin cells of the wood of the Cupressineae in the larger sense. Not all of the canals contain tyloses in the fossilized material, but it is probable that they were universally present in the living tree.

Fig. 10 shows the transition from a vertical to a horizontal duct as seen in vertical radial section. The great difference in size which ordinarily obtains between the two sorts of ducts is very apparent. The abundant tyloses are also a feature of the horizontal ducts, although this phenomenon is also occasionally found in the vertical resin canals.

Vertical traumatic resin canals may extend very far above and below the wound, so that in small isolated pieces of wood their relation to injury is not obvious. From a wide knowledge of living forms of conifers in relation to injury, I am in the position to state inductively that rows of vertical ducts occurring vertically and tangentially in coniferous woods are always due to injury. It has been possible to show that this is the case wherever the material was abundant enough to warrant a definite conclusion.

Horizontal traumatic canals may pass outward from a healed wound through many annual rings. In one instance horizontal canals extended through thirty-eight rings of growth, ending in another

vertical series of ducts, and from this vertical series again other horizontal ducts passed outward beyond the limits of the piece of wood at my disposal. In another case I was able to follow the course of a horizontal duct through over seventy annual rings before it finally tapered off and ended blindly. Although the horizontal canals always start from a vertical series, they by no means always end in the next outward vertical series, even when one is present. More frequently they end blindly, as in the one last described above. The formation of new series of vertical canals may recur in remote rings of growth, and these are nearly always united by horizontal canals.

It will be convenient at this stage to consider more particularly the structure of the wood parenchyma, since it is of considerable diagnostic importance. Our *fig. 2* shows the scantiness of the parenchyma as seen in transverse section through the wood, and also that it occurs on the face of the summer wood. Both these features are unusual, for in the living Sequoias the resiniferous parenchyma is particularly abundant and is found throughout the annual ring. Our fossil also presents a contrast in this respect to the woods of other extinct Sequoias. PENHALLOW[4] describes his *S. Langsdorfii* as having abundant resin cells throughout the annual ring and appearing also in a rudimentary form on the face of the summer wood. In another species, *S. Burgessii*, according to this author,[5] resin cells abundant throughout the ring are most numerous on the face of the summer wood. In the *S. magnifica* of KNOWLTON[6] the distribution of resin cells throughout the annual growth seems to be somewhat uniform. Longitudinal sections of the wood of the species under discussion, taken in numbers both in the tangential and radial planes, show clearly that the absence of resin cells from all locations except the face of the summer wood is not due to disappearance through decay, for there is no evidence of the existence of parenchymatous elements elsewhere than on the face of the summer wood. *Fig. 11* shows the appearance of the resin cells of our species in longitudinal section. They are long narrow elements comparable among living species to those of *S. gigantea*

[4] PENHALLOW, D. P., Notes on Tertiary plants. Trans. Roy. Soc. Canada **9**.

[5] *Op. cit.*

[6] KNOWLTON, F. H., Geology of the Yellowstone Park. Monographs of U. S. Geological Survey **32**: pt. 2.

rather than to the stouter, shorter similar elements of *S. sempervirens*. They may be seen on the outside of the summer wood in two contiguous annual rings. They contain a very small number of resinous globules. On the left of the figure is a longitudinal section of a vertical resin canal.

In *fig. 12* is seen a longitudinal section of a medullary ray of the species under consideration. The lateral walls of the ray which are in contact with the tracheids are characterized by so-called bordered pits, which owe their double contour to the fact that the outline of the pit on the side of the tracheid is different from that on the side of the medullary ray cell. The medullary ray of the present species of Sequoia is strikingly different from that of the two living species in features other than the crucial one of the lateral bordered pits. There are distinctly differentiated marginal cells, broader than the central cells and having two to three radial rows of pits instead of the single row found in the central cells. The marginal cells are further particularized by their undulating borders, the tops of the undulations corresponding to the walls of the tracheids. They present an additional contrast to the central cells in the fact that they are generally without tanniniferous contents and often contain very large clinorhombic crystals, lodged in cysts derived from the cell wall. The presence of crystals finds a parallel in the genus Abies among the Abietineae. STRASBURGER has noticed their occasional presence in *Abies pectinata*. I have found them to be very numerous in *A. concolor* and fewer in *A. grandis*, *A. bracteata*, *A. nobilis*, and *A. magnifica*. In Abies the crystals may or may not be associated with a dark brown matrix similar to that found in the resin cells of cupressineous woods and in the so-called crystallogenous cells which occur in the phloem of many of the Coniferales; but I have not found them inclosed in cysts derived from the cell wall as they are in the fossil species of Sequoia here described. Where the medullary rays are very deep the specialized marginal cells, instead of constituting a single row on the upper and lower borders of the ray, as is shown in our *fig. 12*, may be present to the number of three or four rows. In deep rays specialized cells may also occur in the middle of the ray, just as is occasionally the case with the tracheidal cells in the rays of certain Abietineae. Another feature which differentiates our species

from the living species of Sequoia is the very abundant pitting of the tangential walls of the medullary ray cells. This is an additional point of resemblance to the Abietineae. Through the kindness of Professor PENHALLOW I have had the opportunity of examining the type specimens of his *Sequoia Langsdorfii* and *Sequoia Burgessii*. The state of preservation of the medullary rays is very indifferent in these species; but so far as could be made out they do not possess the peculiar marginal cells and the strong pitting of the terminal (tangential) walls which are characteristic of our species. The *Sequoia magnifica* of KNOWLTON has badly preserved medullary rays, according to the author's description.[7] Professor PENHALLOW has seen sections of our species and agrees that it is new and unlike any which have been described. The name *Sequoia Penhallowii* is proposed for it in recognition of Professor PENHALLOW'S great services to the paleobotany of the Coniferales. The following is the diagnosis:

Sequoia Penhallowii, n. sp.

Transverse.—Rings of growth rather narrow, with sharply marked but thin summer wood. Rings regular, or if varying in thickness varying uniformly and without violent transitions except as the result of injury. Resin canals present in both the vertical and horizontal planes apparently only as the result of injury. The resin canals when present surrounded by resin cells, containing dark brown resin. Resin cells inconspicuous and confined to the face of the summer wood, except in the case of injury, where they may be present throughout the zone of annual growth. Tracheids of the spring wood very large and with pits on the radial walls only. Tracheids of the summer wood with tangential pits.

Radial.—Rays without tracheidal cells, but with distinctly differentiated marginal cells. Lateral pits of ray cells elliptical and bordered, larger in marginal cells. Rows of pits single in the central cells of the ray and two to three seriate in the marginal cells. Medullary ray cells covering one to four tracheids, the central ones resiniferous, the marginal generally empty, sometimes containing large clinorhombic crystals inclosed in cysts derived from the cell walls. Marginal cells with undulating free border, deeper than central cells. End walls of the cells of the medullary rays very strongly pitted. Longitudinal walls of ray cells also pitted and rather thick. Rays contain resin canals in the case of injury, which take their origin from similar vertical canals running in the wood. Resin canals of the rays sometimes ending blindly and sometimes in a more external series of vertical canals, often extending through many annual rings, varying greatly in size and frequently occluded by tyloses. Spring tracheids generally with two rows of opposite pits, which often alternate in the ends.

[7] *Op. cit.*

Tangential.—Rays of one kind only in uninjured parts of the wood. Fusiform rays present with linear rays in the case of injury and varying greatly in size. Fusiform rays when present generally with central resin canal, which is often occluded by tyloses. Linear rays varying greatly in depth. No pits on the tangential walls of the spring tracheids. Pits on the tangential walls of the summer tracheids numerous, generally not in rows.

CONCLUSIONS.

The greatest interest connected with the study of any extinct species is the light it throws on the structure and relationships of living forms. In the case of *Sequoia Penhallowii* the first point in this connection is its affinity with the living species of the genus. The very regular rings of growth and the very thin summer wood find their nearest parallel in *S. gigantea.* It is possible, however, that this similarity in structure of the wood may be due only to a similar mountainous habitat, since such surroundings tend, as is well known, to produce regular growth rings in living trees. For example, wood of spruce grown at high altitudes is particularly fitted for turning and the manufacture of fiddles on account of the regularity of the annual rings. The narrowness of the zone of summer wood, however, cannot be explained in this fashion. The long narrow resin cells of the wood in our species also most nearly resemble those of *S. gigantea.* The wide spring tracheids with their double rows of radial pits present a feature of resemblance to *S. sempervirens* rather than to *S. gigantea;* but this feature cannot be regarded as conclusive, since in some of the fossil Sequoias known only by impressions the larger free leaves of the *S. sempervirens* type were correlated with cones likes those of *S. gigantea.* The greater transpiration thus indicated may well have been provided for by broader and more numerously pitted tracheids. A very strong argument for the association of our species with *S. gigantea* is the fact of their similarity of geographical distribution, for the fossil under discussion came from a cañon of the Sierra Nevada Mountains, which are the home of the living *S. gigantea.* The weight of evidence seems to point to *Sequoia Penhallowii* being somewhat more closely allied to *S. gigantea* than to *S. sempervirens.*

We may now turn to the question of the light which the study of the present species throws on the general problem of the phylogeny

of the Coniferales. Attention has been called in the descriptive part of this article to the striking points of structural resemblance presented by *S. Penhallowii* to certain abietineous species. The medullary rays, for example, although they lack the marginal tracheidal cells characteristic of the typical Abietineae, have distinctly differentiated marginal cells which find a close parallel in the medullary rays of the genus Abies. Further, the marginal cells of the medullary rays of our species are crystallogenous, as are those of Abies. Another feature of strong resemblance to the Abies and the Abietineae is the marked pitting of the terminal walls of the medullary ray cells. This character is absent or poorly marked in the cupressineous series. Equally strong indications of abietineous affinities are to be found in the structure of the wood. The resin cells, which are such a marked feature of cupressineous woods, are almost absent in our species. The few which are present are confined to the outer surface of the summer wood, as in the abietineous genera Tsuga and Abies. The strongest argument, however, for the transitional nature of our fossil is that presented by the ligneous resin ducts. As has been pointed out in the foregoing paragraphs, resin canals occur in both the horizontal and vertical planes in the wood of *S. Penhallowii* as the result of injury. In this feature it presents a striking resemblance to the normal state of affairs in the abietineous genera Pinus, Picea, Pseudotsuga, and Larix. In another place[8] I have pointed out that the normal occurrence of vertical resin canals in the wood of the cone, cone scales, peduncle, and *first* year's growth of strong branches of sexually mature trees of *S. gigantea* is good evidence that this species had come from ancestry characterized by the presence of ligneous resin canals. In both *S. gigantea* and *S. sempervirens* resin canals of the vertical type only occur in the secondary wood as the result of injury. In view of the conditions found normally in *S. gigantea* in the matter of the occurrence of resin canals, I have argued that traumatic resin canals are a case of reversion in the injured wood of *S. gigantea* and *S. sempervirens*. Here we have an example of the value of experimental morphological evidence when confirmed by that of comparative anatomy. Further it may be pointed out that

[8] JEFFREY, E. C., The genus Sequoia. Memoirs of the Boston Society of Natural History **5**: no. 10.

if it is possible to recall experimentally morphological characters, which have entirely disappeared (as in the case of the ligneous resin ducts of *S. sempervirens*), the range of possibility in tracing phylogenetic relationships will be greatly extended. In our fossil the traumatic resin ducts occur in both the horizontal and the vertical planes, and thus present a very close approximation to the condition occurring normally in Pinus. There is, however, a difference in the arrangement of the canals, for in Pinus they are distributed regularly throughout the wood and form an anastomosing system, while in *S. Penhallowii* the vertical canals are confined to remote annual rings and the horizontal canals form a very incomplete system of connecting commissures. It is interesting to note that *S. Langsdorfii* as described by PENHALLOW has only vertical canals, while *S. Burgessii* described by the same author has only radial ones. Had the material of the latter species been as abundant and as easily manipulated as in the case of our fossil, I am disposed to think that vertical canals would have been found as well. It is a noteworthy fact that in three out of the four woods of fossil Sequoias which have been recently described, resin canals similar to those of the Abietineae have been found; or, to state it in another way, the oldest woods of Sequoia of which we have any reasonably complete knowledge more nearly approximate in structure the wood of the Abietineae than do those of their living descendants. This fact, taken in connection with the great geological age of the Abietineae, makes it very probable that the Sequoias, and as a consequence the Cupressineae in a broader sense, have come from an abietineous ancestry. This conclusion is quite in harmony with evidence derived from the study of the female cone, and other important data, as I have pointed out at length in a forthcoming memoir on the Abietineae.

SUMMARY.

A fossil Sequoia from the Auriferous Gravels (Miocene) of the Sierra Nevada Mountains, although presenting features of wood structure which unite it with the living Sequoias, possesses other features which strongly suggest the Abietineae. The paucity of resin cells present only on the outer face of the summer wood, the highly developed medullary rays, and the traumatic resin canals

running both in the horizontal and vertical planes point strongly toward the Abietineae. The species is new and has been named *Sequoia Penhallowii*. It appears to be more closely allied to the living *S. gigantea*, and has, moreover, the same geographical occurrence. A formal diagnosis is given in the body of the article.

In conclusion I wish to express my obligations to Professor R. T. JACKSON for permission to investigate the material described in this article, and to Professor D. P. PENHALLOW for the opportunity of examining his type slides of fossil Sequoias.

HARVARD UNIVERSITY.

EXPLANATION OF PLATES XVIII AND XIX.

PLATE XVIII.

FIG. 1. Transverse section, including several annual rings and showing both horizontal and vertical resin canals in *Sequoia Penhallowii*. × 30.

FIG. 2. Transverse section of thin growth rings of same species. × 180.

FIG. 3. Tangential section of the same showing horizontal resin ducts. × 8.

FIG. 4. Transverse section through a healed wound in the wood of the same species; on the right is a horizontal traumatic resin duct; smaller traumatic ducts can be seen in the spring wood of the three annual rings abutting on the wound. × 4.

FIG. 5. Part of another section through the same wound, showing three horizontal ducts on the left; the smaller vertical ducts of the spring wood can be more clearly seen on account of the greater magnification. × 8.

FIG. 6. The central region of still another section through the same wound showing small vertical ducts in the spring wood. × 8.

PLATE XIX.

FIG. 7. Another of the same more highly magnified from the margin of the wound. × 16.

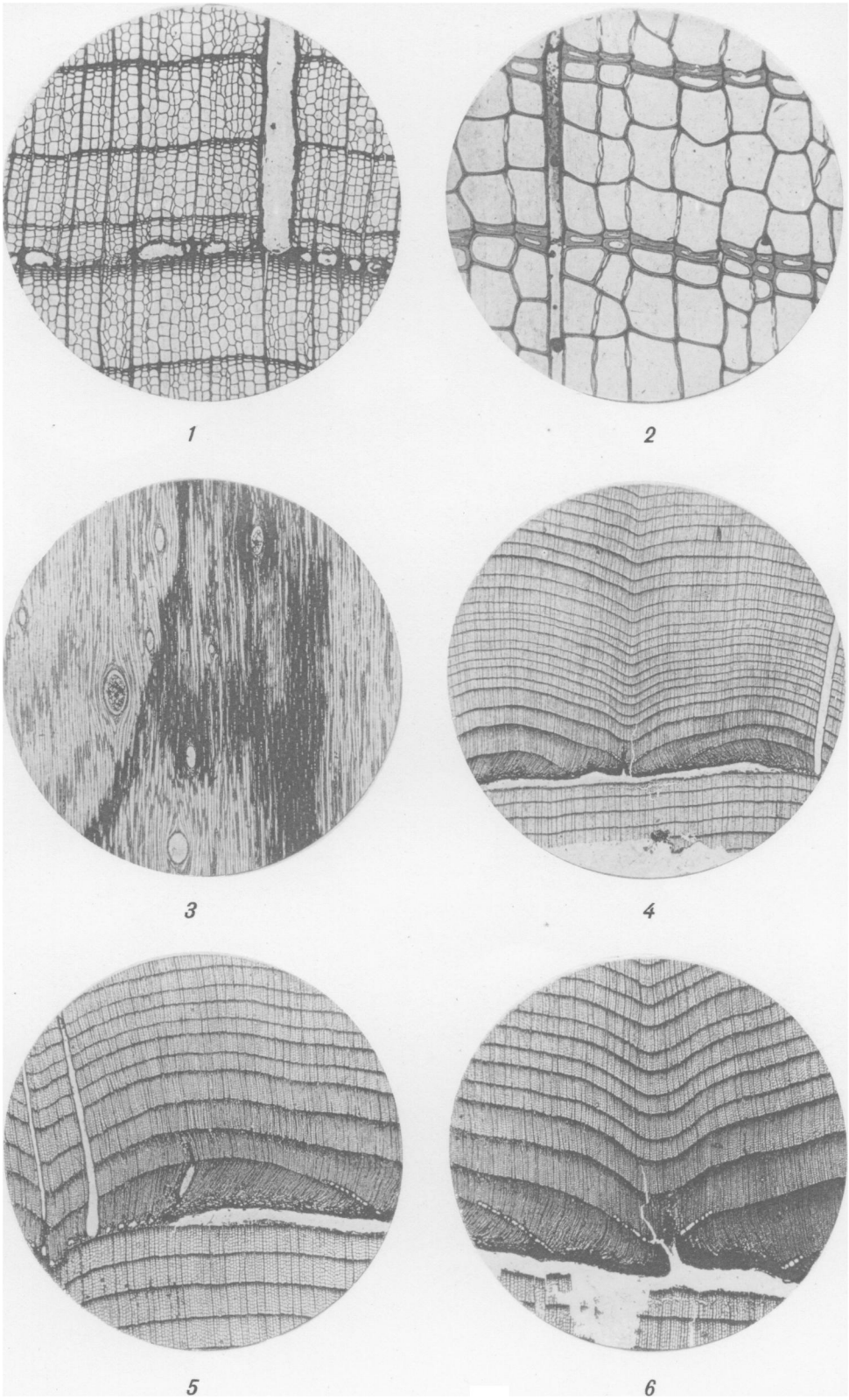
FIG. 8. Transverse section through one of the large horizontal ducts seen in *fig. 3*. × 40.

FIG. 9. Section through a smaller duct from the same preparation as that illustrated in the last figure. × 60.

FIG. 10. Section showing the relation between a horizontal and a vertical duct; the former is blocked by a tylosis. × 50.

FIG. 11. Longitudinal section, showing the scanty resiniferous parenchyma on the face of the summer wood in two annual rings; a vertical resin canal is also shown. × 60.

FIG. 12. Radial section to show the topography of a medullary ray of medium size: on the borders of the ray can be seen the empty crystallogenous cells. × 60.



JEFFREY on SEQUOIA.

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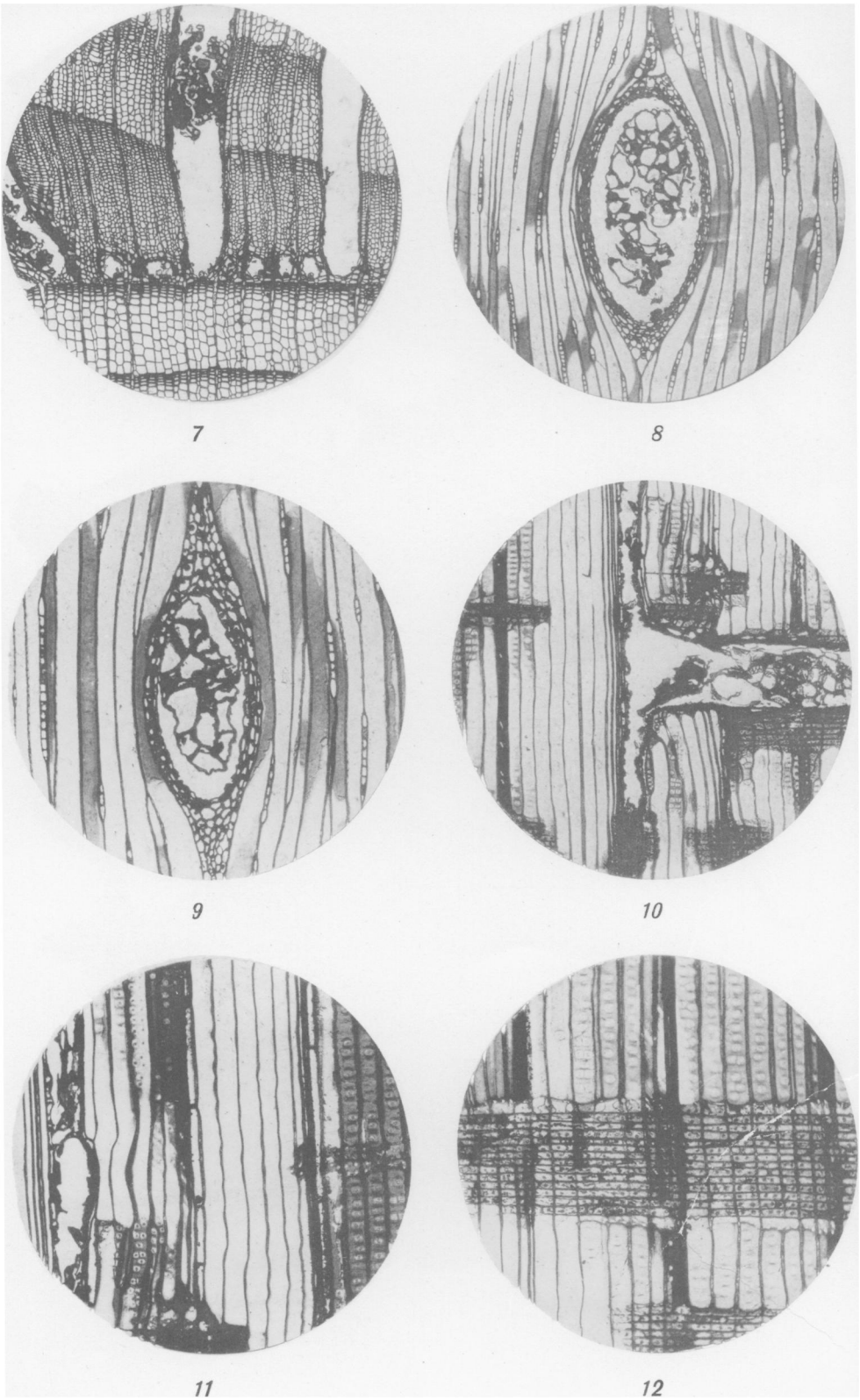

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